

39. Modeling the Differential Sensitivity of Loblolly Pine to Climatic Change Using Tree Rings

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The Southwide Pine Seed Source Study (SPSSS) was undertaken in 1951 to determine to what extent inherent geographic variation in four southern pine species (loblolly pine, *Pinus taeda* L.; slash pine, *P. elliottii* Engelm. var. *elliottii*; longleaf pine, *P. palustris* Mill.; and shortleaf pine, *P. echinata* Mill.) is related to observable geographic variation in climate and physiography. The study's design was based on the classic common garden test design wherein all geographic sources were planted together at multiple sites across the natural range; and the fundamental objective was to test the widely accepted hypothesis that local seed sources were uniformly better adapted and faster growing than nonlocal seed sources from the same species (complete study details appear in Wells and Wakeley, 1966).

Recently, there has been increasing interest in the SPSSS and other similarly designed studies because these studies offer long-term data that could be useful in assessing genetic sensitivity of tree species to climatic effects. The common garden design allows a comparison of the responses of different individual genotypes and seed sources to the same climatic regime at one common site. Moreover, the existence of many planting sites—all with the same seed sources colocated—provides an opportunity to assess the effect of changing climatic regimes on the same seed sources. Thus, the tree-ring analysis of the SPSSS could provide unique information about the sensitivity of the four southern pine species to future climatic changes resulting from greenhouse warming in the southeastern United States (e.g., Rind et al., 1990).

In this chapter, we examine this potential for one of the SPSSS species: loblolly pine. Specifically, we hope to determine the degree to which different seed sources located at the same plantation differ in their responses to the same local climate regime. Any identified differences could be the result of local adaptations of the seed sources being investigated. In turn, these indicated local adaptations might be used to determine these seed sources that are apt to perform best under various scenarios of future climatic change.

The Southwide Pine Seed Source Study Plantations

Originally, the loblolly pine portion of the SPSSS consisted of fifteen provenance plantations containing between eight and fifteen seed sources collected from locations across the natural range of the species. Of the fifteen original plantations, only eight have survived to the present time. Figure 39.1 shows the locations of these eight surviving plantations, along with the locations of the seed sources used. From this map, it is apparent that this subset of original plantations still covers most of the geographic range of loblolly pine. A key to these plantations is also provided in Table 39.1, by both original SPSSS plantation code and geographic name. Similarly, a key to the seed sources is provided in Table 39.2, again by original SPSSS code and geographic name. These SPSSS plantation and seed source codes will be used throughout this paper.

The seed sources and plantings used in the SPSSS were actually divided into two series, Series-1 and Series-2, mainly to avoid the overwhelming task of planting large plots of all fifteen seed sources at all locations (Wells, 1983). The Series-1 plantings are found in all but one of these plantations, the exception being located in northern Mississippi (see Figure 39.1), which only has Series-2 trees. In contrast, Series-2 trees are present at only five of the eight surviving plantations. Thus, four of the eight plantations have both series present.

At each plantation, each seed source was planted in four randomized complete blocks containing 121 trees in an 11×11 grid (Wakeley, 1961; Wells and Wakeley, 1966). The inner forty-nine trees laid out in a 7×7 grid were used for remeasurement, with the remaining trees were used as border or buffer trees between plots. Over the years, a large amount of natural mortality and some prescribed thinning occurred. Therefore, the number of trees ultimately sampled for tree-ring analysis was a small fraction of the original total planted. This fact should not be viewed as a drawback, however, because the sampled trees were the survivors of a (largely) natural winnowing-out process that occurs in natural, unmanaged forests as well.

Summaries of mortality, growth, and yield have been published several times over the past forty years (Wakeley, 1953, 1959, 1961; Wells and Wakeley, 1966; Nance and Wells, 1981; Wells, 1969, 1983), as well as reports on insect and disease data (Henry, 1959; Henry and Coyne, 1955; Henry and Hepting, 1957; Wells and Switzer, 1975). These data generally show clear genetic differentiation between geographic sources in response to major climatic and physiographic

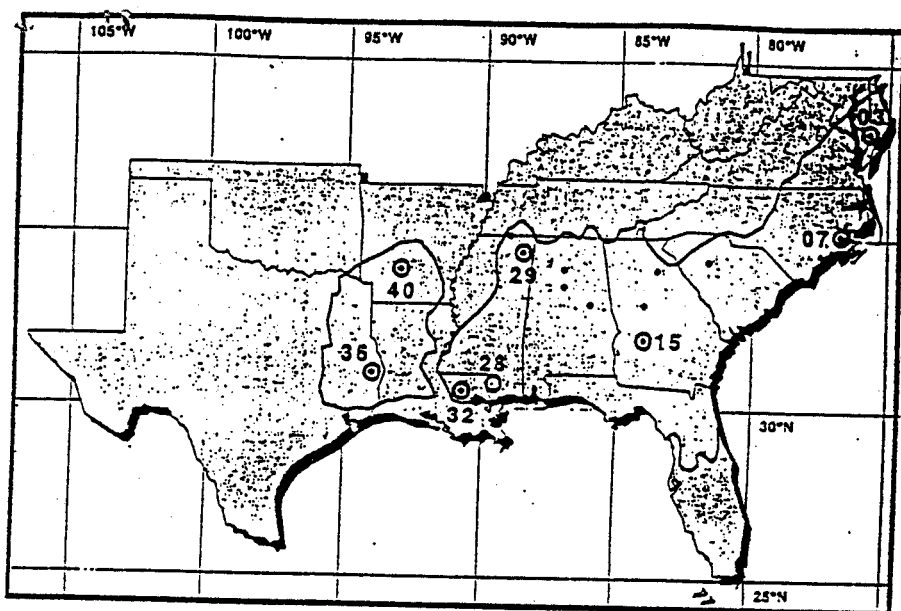


Figure 39.1. A map of the SPSSS plantation and seed source locations. The large open circles are the eight existing plantations sampled for this study. (See Table 39.1 for the plantation codes.) The small, filled circles are the locations of the fifteen seed sources used in the SPSSS. (See Table 39.2 for a listing of those sources.) When a small filled circle falls inside a large open circle, that plantation has a local seed source. The irregular lines on the map delineate the general range boundaries of loblolly pine.

effects, with much smaller amounts of genetic variation within the major climatic and physiographic regions.

The original data collections on the SPSSS were spaced at five-year intervals, which is generally not frequent enough for detection of climatic effects in the southern and southeastern United States. However, it was possible to obtain increment cores from the living trees in the study and obtain direct measurements of annual radial increment. These measurements provided the basis for the data presented and analyzed in this chapter.

Table 39.1. The SPSSS Loblolly Plantations

Plantation Code	Geographic Region
03	Maryland, eastern
07	North Carolina, eastern
15	Georgia, southwestern
28	Mississippi, southern
29	Mississippi, northeastern
32	Louisiana, southeastern
36	Texas, eastern
40	Arkansas, southwestern

Table 39.2. The SPSSS Loblolly Pine Seed Sources¹

Seed Source	Series	Geographic Region
301	1	Maryland, eastern
303	1,2	North Carolina, southeastern
305	1	North Carolina, eastern
307	2	South Carolina, western
309	1	Georgia, southwestern
311	2	Georgia, northeastern
315	1	Alabama, northern
317	2	Alabama, northeastern
319	1	Alabama, northern
321	2	Mississippi, northeastern
323	1,2	Louisiana, southeastern
325	1	Texas, eastern
327	1,2	Arkansas, southwestern
329	2	Tennessee, western
331	2	Georgia, northwestern

¹ Note the three common seed sources in the two Series.

Climatology of the Southwide Pine Seed Source Study Plantations

To place this study in its proper climatological context, comparisons of plantation monthly precipitation and temperature climatologies were made. Figure 39.2 shows the mean monthly maximum and minimum temperature and total monthly precipitation profiles for the eight SPSSS plantations. These monthly profiles are based on $1^\circ \times 1^\circ$ grid-point data from the Richman-Lamb climatological database (Lamb, 1987), covering the period from 1949 to 1988. The grid-points closest to the plantation locations were used. In the case of plantations 28 and 32, the closest grid-point fell roughly equidistant between the two. Consequently, the same climate data were used for each of these plantations.

The maximum temperature profiles (Figure 39.2A) indicate a temperature range of 6 to 16 °C in January, and 30 to 34 °C in July, across all plantations. This indicates generally higher variability in winter maximum temperatures across the plantations, a result consistent with continentality of climate. The profiles also reveal a surprising degree of warm-season concordance. That is, for six of the eight plantations, there is little difference in maximum temperatures during the warm-season months of May to September, the season when the most radial growth of loblolly pine should occur. For the six warmest plantations, warm-season maximum temperatures average at approximately 32 °C. In contrast, the two anomalous plantations, 03 and 07, are the most northerly plantations of the group and have warm-season temperatures that are 3 to 4 °C cooler on average. Only for the cool-season months of November to March is there a clear separation of the plantations into essentially three groups, which are 1) 15, 28, 32, 36; 2) 07, 29, 40; and 3) 03, ranked from warmest to coldest, respectively. This stratification is roughly by latitude, with the warmest cool-seasons occurring at the most south-

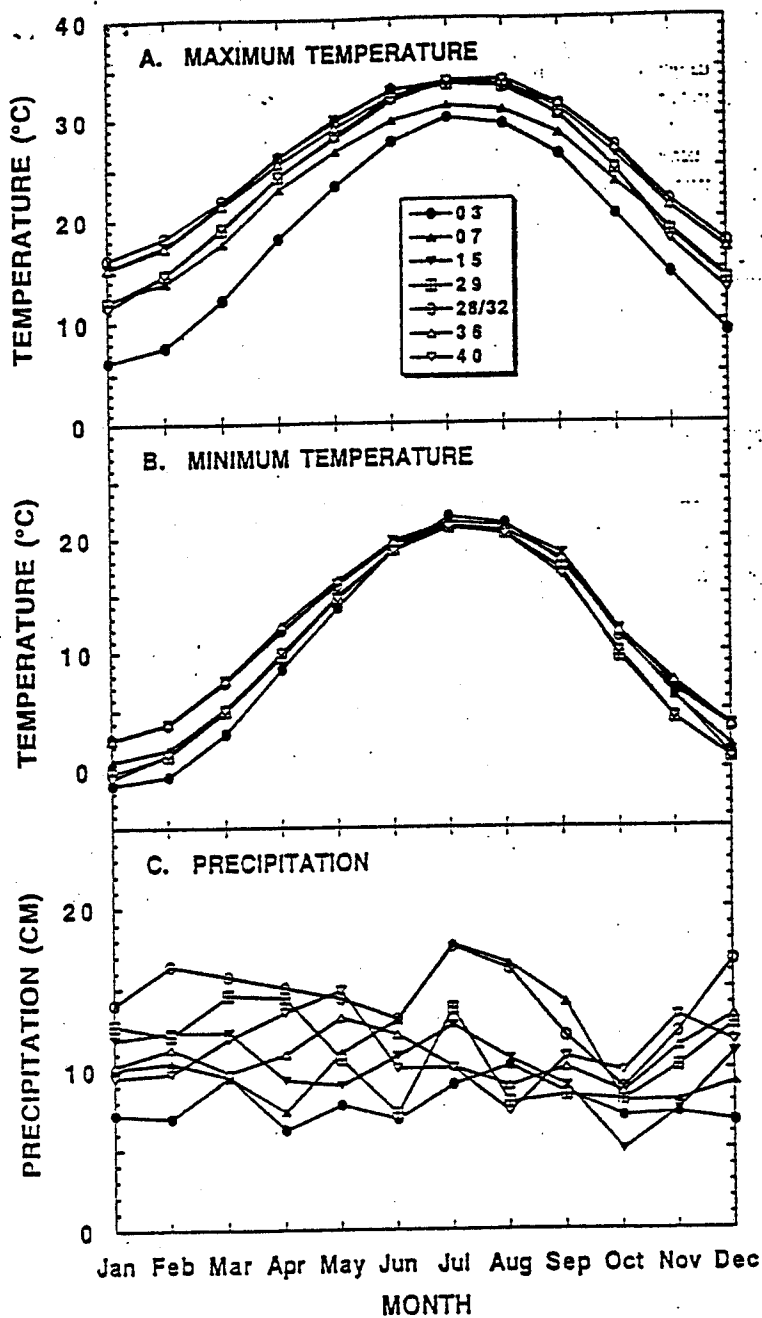


Figure 39.2. The mean monthly maximum and minimum temperature and total monthly precipitation profiles of the eight SPSS plantations.

early plantations. As before, plantation 03 is most anomalous, with cool-season temperatures that average 5 to 7 °C below the other plantations. The significance of this phenomenon will become apparent in the climate modeling of the tree-ring series, described later in this chapter.

The minimum temperature profiles (Figure 39.2B) reveal far less variability between plantations. None of the plantations separate out during the growing season months. Only for the cool-season months of January to March is there a clear separation by latitude into the three described groups, but this separation is much smaller for minimum temperatures. Additionally, only in January do any of the plantation minimum temperatures fall marginally below the freezing mark.

The precipitation profiles (Figure 39.2C) indicate that rainfall is evenly distributed throughout the year across all plantations. Only plantation 07 has a regime that is weakly warm-season dominant. Plantation 03 is the driest with an average of about 8 cm/month; plantations 28 and 32 are the wettest with 14 cm/month. All other plantations receive at least 10 cm/month of rainfall.

From this analysis, it is clear that the SPSSS loblolly pine plantations are located in generally warm, moist environments. The most anomalous is plantation 03 located at the northern limit of loblolly pine distribution, which is comparatively cool, dry. Given this exception, the lack of any strong latitude-based differences in climate during the warm-season/growing-season months suggests that loblolly pine "chooses" to grow in a reasonably homogenous regional climate regime (i.e., warm and moist). This means that it could be difficult to find strong differences in the strength of the climatic response in the tree rings, either within or between plantations, because the climate variables influencing growth may be equally limiting to the various seed sources across the range. However, this does not rule out significant differences in which climate variables are most influential on growth because of changing site characteristics (e.g., site hydrology, soil type, fertility) and as the plantation climatologies change geographically (cf. plantations 03 and 07 with the others).

The Southwide Pine Seed Source Study Tree-Ring Database

Between 1952 and 1953, a total of 18,718 loblolly pine trees were planted on the fifteen original SPSSS plantations. Through attrition, by natural and anthropogenic causes, both plantations and trees suffered significant losses. Thus, in the eight plantations surviving today, only 1,634 trees remain. These remaining plantation trees were completely sampled for increment cores between 1990 and 1991.

Two increment cores, diametrically opposed to each other, and passing as near as possible through the pith, were collected from every surviving tree. This was facilitated by the use of a gasoline-powered increment borer that was able to extract a full-diameter, 5-mm core from a tree in less than thirty seconds. Because the objectives of this study emphasized tree growth over the entire period of the plantations since establishment, cores were collected from as low on the stem as possible.

In the lab, the increment cores were processed using standard dendrochronolo-

logical techniques (e.g., Stokes and Smiley, 1968; Fritts, 1976; Cook and Kai-riukstis, 1990). The cores were firmly glued into grooved sticks with the long axis of the cells oriented vertically, sanded to a high polish, and the ring widths carefully cross-dated (Krusic et al., 1987). After measurement to a precision of ± 0.01 mm, the ring-width series were checked for cross-dating quality using program COFECHA (Holmes, 1982). Each seed source collection and plantation was processed independently of all others to ensure that the dating and measuring procedures were unbiased. Although some tree-ring data were available prior to 1960, a combination of planting shock and juvenile growth effects made the pre-1960 ring-widths highly erratic between trees. Therefore, all analyses presented here only used tree-ring data since 1960.

Trees of each seed source, from all eight plantations, were separated into two distinct stand-canopy classes. Dominant and codominant trees of a seed source were grouped as one class, and those remaining were grouped into a subdominant or suppressed class. The selection criterion for the purposes of this partition was tree diameter, with the five largest diameter trees from each plot considered the dominant-codominant trees. (Tree heights were not available at the time of sampling.) This number was justified by noting that it approximated a stocking level of 40 trees/hectare, which is typical for stands of mature loblolly pine. In the plots that had more than five surviving trees, those smaller than the five largest were considered subdominant or suppressed. Only the dominant-codominant trees were used in the subsequent tree-ring analyses on the basis that these are the ultimate survivors that truly matter. Another rationale for deleting the subdominant-suppressed trees was the way in which radial growth became extremely compressed in some of those trees for some years, which was not the case in the dominant-codominant trees growing on the same plot. Consequently, there was concern that the climate signal in the tree rings of the subdominant-suppressed trees might be confounded by competition-related effects.

Table 39.3 has the tally of cores and trees per plantation that fell into the dominant-codominant category used here. The total number of trees is 1,537, which is 94% of the total trees available. Therefore, little information was lost, in any event, by deleting the trees considered subdominant or suppressed.

Table 39.3. Southwide Pine Seed Source Study Loblolly Pine Plantation Series-1 and Series-2 Dominant-Codominant Core Collection

Plantation code	#Cores	#Trees
03	280	218
07	456	289
15	278	170
28	273	161
29	223	126
32	419	249
36	137	72
40	454	252
Total	2,520	1,537

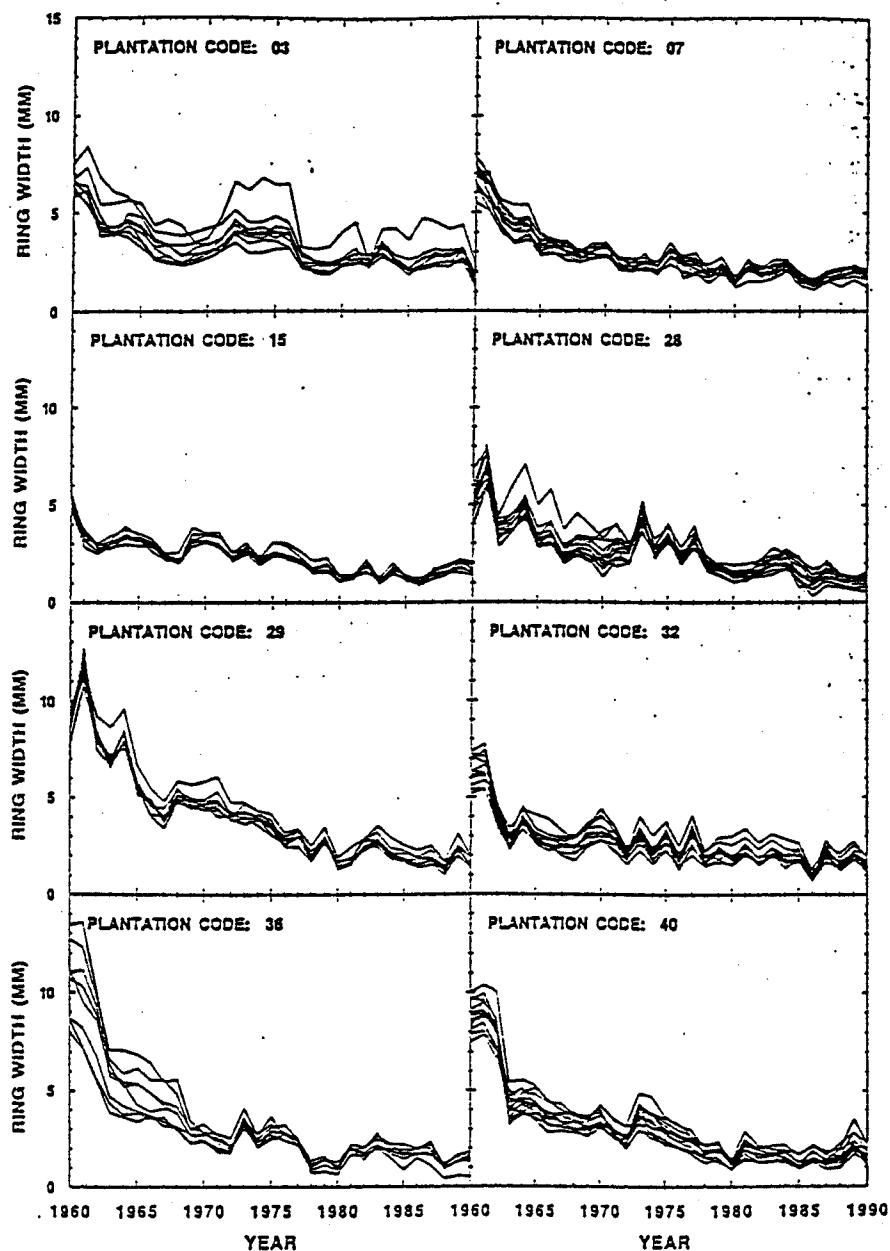


Figure 39.3. The seed source mean ring-width chronologies for each of the eight SPSSS plantations. Note the generally high level of conformity between seed sources at each plantation.

The Southwide Pine Seed Source Study Loblolly Pine Tree-Ring Chronologies

Figure 39.3 shows plots of the mean dominant-codominant ring-width chronologies for all seed sources present at the eight plantations. The overlays of the seed source chronologies are intended to illustrate the degree of homogeneity in the overall trajectory of radial growth within each plantation. With the exceptions of plantation 36, which shows considerable variation between seed sources up to 1970 but excellent convergence thereafter, and the odd seed sources in plantations 03, 28, and 29, the within-plantation seed source mean ring-width chronologies are remarkably similar. The odd behavior of individual seed sources in plantations 03, 28, and 29 may be the result of a combination of genetic and silvicultural factors that affected changes in stocking level and, consequently, growth rate over time. For example, the anomalous seed source in plantation 03 maintained a higher radial growth rate presumably because it had the lowest stocking level of any of the seed sources. This could have occurred from a combination of a higher rate of natural self-thinning and prescribed thinning. Regardless, such factors could wholly obscure any differences in growth resulting from seed source-related differential responses to climate. Consequently, it is necessary to remove absolute growth-rate effects from the tree-ring data.

The removal of absolute growth-rate effects was accomplished by modeling the trajectory of each individual ring-width series with a modified negative exponential curve of the form:

$$G_t = ae^{-bt} + k \quad (1)$$

in which G_t is the growth-curve estimate, a is the intercept, b is the slope, k is the asymptotic growth rate for over-mature trees, and t is time in years (Fritts et al., 1969). An examination of the mean ring-width plots in Figure 39.3 indicates that this model is reasonable for estimating the curvilinear growth trends apparent in the data. So, a modified negative exponential curve was fit to each individual ring-width series and the growth trend removed as:

$$I_t = R_t/G_t \quad (2)$$

in which R_t is the actual ring width, G_t is the growth curve value, and I_t is the resultant tree-ring index, for all years $t = 1, n$. This process of detrending and transforming the tree ring into dimensionless indices is known as "standardization" (Fritts, 1976) because it tends to equalize the growth variations of trees over time regardless of age, size, or absolute growth rates. Tree-ring indices have a defined mean of 1.0 and typically fall in the range of 0 to 2.

Figure 39.4 shows the mean tree-ring index chronologies for the eight plantations, as in Figure 39.3. The growth trends apparent in the raw data are clearly gone, along with much of the scatter in some of the plantations. For example, the scatter in the mean ring-widths of plantation 36 prior to 1970 is now gone. The

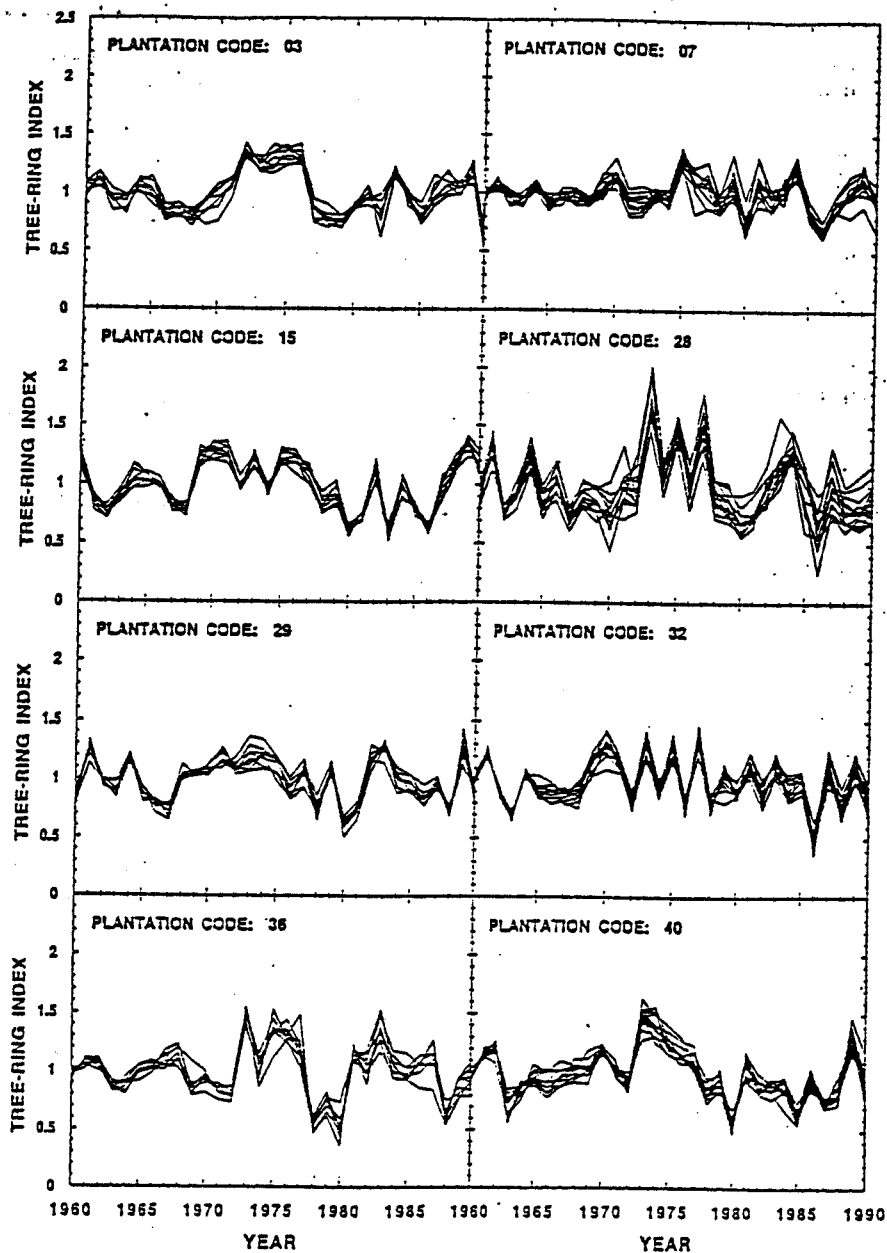


Figure 39.4. The seed source standardized tree-ring chronologies for each of the eight SPSSS plantations. These series were obtained after removing the long-term trends in radial growth from the individual ring-width series. Note that most of the differences between seed sources indicated in Figure 39.3 are now greatly reduced.

seed source anomalies in the ring-width series from plantations 03 and 29 are now also gone. The only clear inflation of differences from ring-widths to indices is evident in plantation 28, principally after 1984. This is related, in part, to the rapid and highly variable growth in the mid-1970s, which caused the end-fitting of the negative exponential curve to be more variable.

The tree-ring indices in Figure 39.4 will be used to ascertain the degree to which differential climate responses exist both within and between plantations. However, before proceeding with the climate modeling, a comparison of certain descriptive statistics will be done. In dendrochronology, four descriptive statistics are frequently computed for interpretive purposes. They are 1) mean sensitivity, 2) standard deviation, 3) serial correlation, and 4) mean between-series correlation.

Mean sensitivity (ms) is a measure of high frequency or year-to-year variability in tree-ring series. It is computed as:

$$ms = \frac{1}{n-1} \sum_{t=1}^{n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right| \quad (3)$$

in which, x_t is the tree-ring value for year t . Mean sensitivity has the interesting property that it assumes effectively the same value whether computed from raw ring-widths or from the same series after standardization to tree-ring indices. This is because it emphasizes the high frequency component of the time series only. The numerator is a first-difference operator, which is insensitive to all but the year-to-year changes in growth. Traditionally, ms has been used as a qualitative tool for estimating the relative sensitivity of a tree-ring series to climatic, environmental influences. High ms values are indicative of trees that are highly "sensitive" to yearly changes in growth-limiting influences. For our purposes, it is used to compare within- and between-plantation tree-ring variability in an effort to see if any unusual differences in "sensitivity" can be found.

Standard deviation (sd) is a classical statistical measure of variability. It is computed as:

$$sd = \sqrt{\frac{1}{n-1} \sum_{t=1}^n (x_t - \bar{x})^2} \quad (4)$$

in which \bar{x} is the arithmetic mean of series x . Different from ms , sd measures variability in a tree-ring series at all time-scales and therefore, it is sensitive to low frequency, multiyear changes in growth as well, which is not the case for ms . In general, $sd > ms$ when positive autocorrelation is present in the series, as is usually the case with tree rings.

Serial correlation (r_1) is a measure of the year-to-year persistence in growth. As such, it is an expression of the physiological preconditioning (Fritts, 1976) that a tree goes through when climatic and environmental influences during one year affect the potential for growth in subsequent years. It is computed as:

$$r_1 = \frac{\sum_{t=2}^n (x_t - \bar{x})(x_{t-1} - \bar{x})}{\sum_{t=1}^n (x_t - \bar{x})^2} \quad (5)$$

In tree-ring series, r_1 is usually positive and in the range $0 < r_1 < 1$, meaning that above-average growth in one year tends to promote above-average growth the following year, and vice versa. In reality, r_1 is only a rough, first-order estimate of chronology persistence. It is well-known that tree-ring chronologies often have more complex persistence structures that are well-modeled as higher-order, autoregressive-moving average processes (Box and Jenkins, 1976). However, as a simple descriptive statistic of persistence in tree-ring chronologies, r_1 is sufficient for our purposes.

Mean sensitivity (ms), sd , and r_1 are roughly related in the following ways. When r_1 goes up, ms goes down, with the converse also true, across the domain $-1 < r_1 < 1$. Also, sd is a complex interaction between ms and r_1 as each contributes to different aspects of the overall variability expressed in sd , especially when $r_1 > 0$.

The mean between-series correlation (\bar{r}_{bt}) is a measure of the strength of the common signal between trees. It is computed as:

$$\bar{r}_{bt} = \frac{\sum_{i=1}^{m-1} \sum_{j=i+1}^m r_{ij}}{m(m-1)/2} \quad (6)$$

in which r_{ij} is the correlation between tree i and j and m is the number of trees. When more than one tree-ring series is available per tree, the number of between-tree correlations is increased accordingly in computing \bar{r}_{bt} . Because tree-ring series are cross-dated before being used in mean chronologies, \bar{r}_{bt} is always in the range $0 < \bar{r}_{bt} < 1$. The mean between-series correlation is an unbiased estimator of the percent variance in common between tree-ring series (Wigley et al., 1986), and, in this sense, is a measure of the strength of the common climatic-environmental signal contained in the record. In the context of this chapter, it serves two purposes. First, it indicates the homogeneity of the within-seed source common signals in each plantation. Second, it indicates the similarity of the common signal strength between plantations. At times, \bar{r}_{bt} has been advocated as an indirect measure of the strength of the climatic signal in tree-ring series. This is based on the argument that as climate becomes more limiting to growth, \bar{r}_{bt} should increase because the trees will be forced to grow more similarly. Although heuristically appealing, the use of \bar{r}_{bt} for this purpose is often disappointing when compared to the "goodness-of-fit" of climate models based on meteorological data.

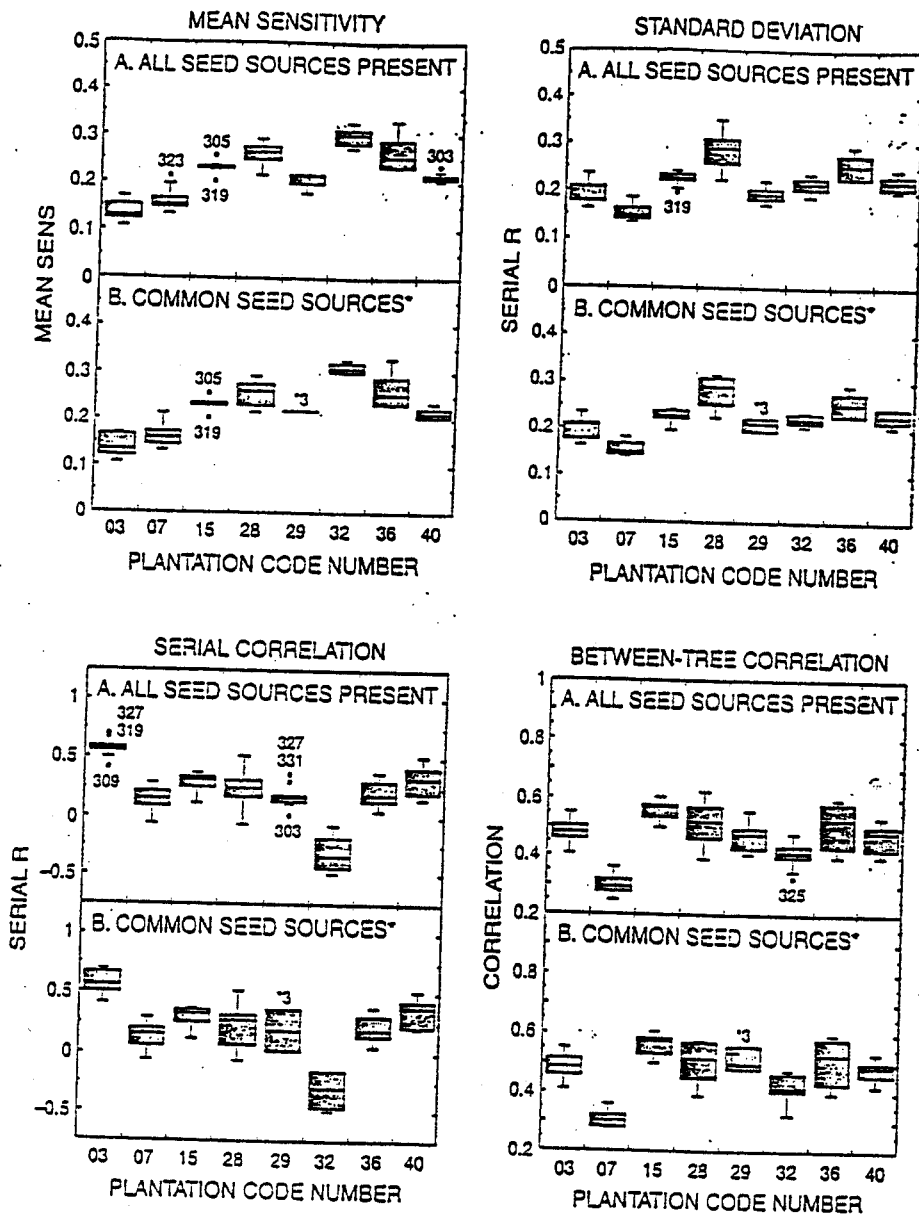


Figure 39.5. Boxplots of tree-ring chronology statistics described in the text. The boxplots were constructed for all seed sources present and for only those in common among all plantations. Note that there is not much difference between the boxplots.

These statistics are compactly displayed as a series of boxplots for all plantations in Figure 39.5. Each boxplot locates the median data value as the horizontal line through the box. The top of the box is the upper quartile (UQ; the data value halfway between the median and maximum value), and the bottom of the box is the lower quartile (LQ; the data value halfway between the median and minimum

value). The length of the box is the interquartile distance (IQD) or $UQ-LQ$, which contains 50% of the sample values. The lines extending above UQ and below LQ are the limits of the data that do not exceed $UQ + 1.5 \times IQD$ and $LQ - 1.5 \times IQD$, respectively. The open dots are regarded as outliers that exceed the upper or lower $1.5 \times IQD$ limits. For each statistic, boxplots were made for all seed sources present at each plantation (a), and for only the eight seed sources common to all plantations (b). The exception to the latter is plantation 29, which only has three of the eight common seed sources because it is made up of only Series-2 trees. The common seed sources are 301, 303, 305, 309, 319, 323, 325, and 327. The common seed source boxplots may provide clearer comparisons between plantations by keeping the seed sources constant.

The boxplots indicate considerable variability in the four statistics both within and between plantations. The variation in seed source statistics within each plantation appears to be consistent with the level of visual scatter seen in some of the seed source tree-ring chronologies shown in Figure 39.4. For example, all of the boxplots for plantation 15 are uniformly narrow, which is consistent with the excellent visual agreement between the seed source chronologies (Figure 39.4). Conversely, all the boxplots for plantation 36 are consistently wider and probably reflect the lesser agreement between seed source chronologies for that plantation. Other plantations give more ambiguous results, witness the narrow ms and wide r_1 boxplots for plantation 32, even with apparently excellent agreement between chronologies. Given the random variability associated with the estimation of such statistics based on only thirty-one observations, it is not possible to determine if such effects are related to differences in seed source genetics.

In contrast, the boxplot comparisons between the plantations indicate the possibility for some plantation-level differentiation. For example, the ms statistics reveal that plantation 03 and, to a lesser degree, plantation 07 have less year-to-year ring-width variability than the other plantations. This may be related to the somewhat cooler maximum temperatures at these sites described earlier, which may reduce the development and severity of internal moisture stress in the trees. In contrast, plantation 32 has the highest ms , although it does not stand out greatly. The sd results are less clear cut, with only plantation 07 maintaining somewhat lower overall variability compared to the rest. Plantation 28 is marginally the most variable as a result in part of the mid-1970s growth pattern described earlier. However, the sd results are partly confounded by variations in r_1 across the plantations. The clearest example is plantation 03, where sd increased relative to plantation 07 even though it has the lowest ms . This result occurred because plantation 03 has the highest r_1 among all plantations and is, again, an anomalous unit. As will be shown later, this is almost certainly caused by a distinctly different response to climate compared to the other plantations. In terms of r_1 , the other odd plantation is 32. In this case, $r_1 < 0$, a highly unusual result in dendrochronology. The reason for this phenomenon is unknown. The \bar{r}_{b_i} boxplots are reasonably uniform across plantations. Only plantation 07 has an anomalously low \bar{r}_{b_i} , meaning that there is unusually high variability between trees, perhaps caused by high variability between the four plots per seed source. This result thus suggests that

the North Carolina plantation plots are not homogeneous with regards to local site conditions. Otherwise, the SPSSS plantations appear to have comparable levels of plot homogeneity.

These classical dendrochronological statistics have revealed some evidence for differentiation between plantations that is at least consistent with some differences in the plantation climatologies (i.e., plantations 03 and plantation 07). Plantation 32 is also anomalous, but for reasons that are not presently explicable.

A More Detailed Look for Seed Source Differences

Although the boxplot results do not, in general, suggest strong differences between seed sources, it is still worth looking more carefully for these effects. The boxplots are rather blunt statistical tools that may be obscuring some true, albeit small, differences. First, we will examine the degree of similarity between the seed source chronologies using principal components analysis (PCA; Cooley and Lohnes, 1971). This will be followed by a very detailed linear modeling exercise using a mixed-effects analysis of variance (ANOVA) model that explicitly utilizes all components of the original randomized complete box design of the SPSSS experiment.

Principal Components Analysis

Principal components analysis was carried out on the seed source chronologies of each plantations. Based on the visual similarities of the chronologies in Figure 39.4, it was anticipated that the majority of the variance would be in common. However, PCA has the capability of decomposing the total variance into orthogonal modes of unique covariance, which could be seed source related. Thus, even though the first dominant mode may explain the majority of the variance in the seed source chronologies, it is possible that significant higher-order seed source modes might also be present.

The results of the PCAs confirmed the visual similarities between the seed source chronologies. In every case, the first PC, which accounts for the most common mode of variation among all series, explained 81.1 to 94.4% of the total variance. In contrast, the second PC, which accounts for the next most common mode of variation among all series, explained only 1.9 to 5.6% of the total variance, a result not statistically significant ($p < .10$) using a Monte Carlo testing procedure (Preisendorfer et al., 1981). All remaining higher-order PCs were similarly not significant. The plantation with the highest common seed source signal was plantation 15 (94.4%), followed by 29 (92.6%), 40 (92%), 32 (91.5%), 03 (90.9%), 36 (90.6%), 28 (85.2%), and 07 (81.1%). All of these figures are markedly higher than the \bar{r}_b results in Figure 39.5., in which the average over all plantations is 45.4%, with a range of 24.9 to 62.3%. Thus, there is considerably more variability between trees within provenances than between mean seed source chronologies within plantations. This fact would seem to work against finding seed source level differences in the SPSSS loblolly pine tree-ring data.

Analysis of Variance

The SPSSS employed a randomized complete block design. Specifically, each block consists of eight or nine seed sources composing the particular Series represented at the plantation. Each provenance within a block consists of the surviving individual trees of the forty-nine (7×7) planted spaces. Finally, each individual tree with a provenance consists of the one or two radial tree-ring cores sampled from that tree. This rigorous experimental design facilitates a detailed ANOVA components within and between seed sources using ANOVA techniques. In so doing, the inherent error structure of the randomized complete block design can be properly exploited.

The SPSSS was actually composed of two separate plantings: Series-1 and Series-2. Because the Series-1 planting was the most successful in terms of survival rate and is also present in seven of the eight existing plantations, the decision was made to only use those tree-ring series in the ANOVA. As before, to avoid the possible bias of suppressed trees in the results, the data from only the five largest dominant-codominant trees per plot were used.

The ANOVA was formulated to test for differences between seed sources resulting from climate. The SAS general linear model procedure (SAS, 1985), which allows for unbalanced experimental designs, was used for this purpose. All treatments and their interactions were assumed to be random except for provenances, which were assumed to be fixed. This test was conducted on the tree-ring series after they were first transformed to stabilize the variance, detrended to remove long-term growth trends, and prewhitened to remove autocorrelation. The ANOVA proceeded in a sequential fashion. First, the variance resulting from the endogenous treatments implicit in the randomized complete block design were isolated as sources of variation in the model (Table 39.4). Hence, the original error structure of the experimental design was explicitly evaluated before any climate effects on radial growth were tested. The incorporation of climate effects in the model was designed to maximize the correlation with the tree-ring index, and therefore to maximize information from the available climate data.

The climate index was formulated as a multiple linear regression model predicting tree-ring index, given that the variance resulting from all design components had been factored out. Symbollically, therefore:

$$CI = TRI - (\text{Block} + \text{Provenance} + \text{Plot} + \text{Tree} + \text{Radius}) \quad (7)$$

in which CI = climate index, TRI = tree-ring index, Plot = Block \times Provenance, Tree = tree within Plot, and Radius = radial growth series within Tree. The CI was generated using a stepwise regression technique, with exogenous variables of monthly temperature, precipitation, and Palmer Drought Severity Index (PDSI) for both present and prior growing seasons. The method selected exactly six variables that were maximally correlated with the TRI. The single CI for each plantation represented a common climatic signal among all tree-ring series and provenances. This CI was entered into the linear model as a covariate to remove the common climatic signal before testing for interactions between CI and seed source.

Table 39.4. Example of Analysis of Variance Results for Plantation 28

Factor	% Model SS	Prob > F
Block	< 1.0%	0.95
Provenance	3.5%	0.16
Plot (block \times prov)	1.3%	0.32
Tree within plot	15.9%	0.0001**
Radius within tree	4.4%	0.0001**
Climate index (CI)	69.3%	0.0001**
CI \times block	< 1.0%	0.65
CI \times provenance	1.4%	0.0001**
CI \times plot	< 1.0%	0.23
CI \times tree within plot	2.7%	0.30
CI \times radius within tree	< 1.0%	0.99

** significant at the 1% level

The ANOVA just described was applied to all seven plantations containing Series-1 plantings. This represents all but plantation 29 in northern Mississippi. In five of the seven plantations, a significant CI \times Provenance interaction remained in the residual tree-ring chronologies after the design variables and common climatic signals were removed. The two plantations not showing a significant CI \times Provenance interaction were 40 and 32. The negative result for Plantation 40 was unexpected given its extreme western location. Regardless, these results suggest a differential response of these loblolly pine provenances to the same set of climatic conditions. Table 39.4 provides a detailed breakdown of the model results for plantation 28 as an example. The variance accounted for by the CI \times Provenance interactions, although statistically significant in most cases, always accounted for less than 2% and usually < 1% of the total variance of the overall ANOVA models of the plantations. The statistical significance of such small percentages is caused by the very large degrees of freedom available for each test (e.g., 3,712 for plantation 28). Hence, the practical significance of these results is probably not meaningful.

The results thus far suggest little evidence for strong seed source differences within the plantations. Small, yet statistically significant, differences between seed sources can be found in some of the plantations. However, these differences typically account for only < 2% of the total variance among all seed sources, which gives them little operational significance. Consequently, the climate modeling described next will be based on pooling the common variance among seed sources using PCA.

Climate Response Models for the Southwide Plant Seed Source Study Plantations

Using the climate data described earlier, simple correlation analyses were carried out on the time series scores of the first tree-ring PC from each plantation. The

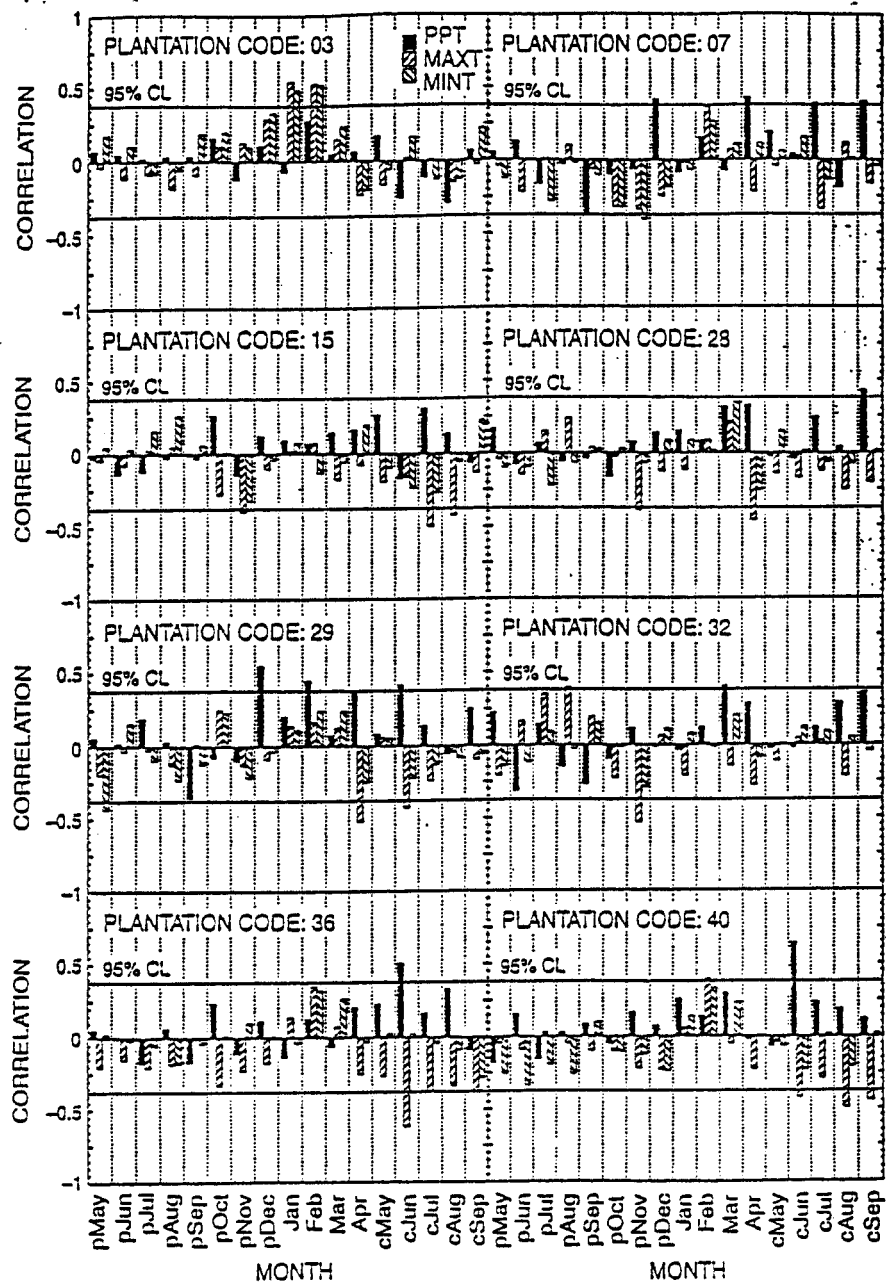


Figure 39.6. Correlations between loblolly pine tree rings and monthly climate over the period from 1960 to 1988. In each case, the tree-ring series used for correlation with climate was the first principal component of the plantation seed source chronologies. This represents the most common mode of covariance between seed sources and is the only orthogonal mode that is statistically significant.

correlations were estimated over the common period of 1960 to 1988 using a dendroclimatic year (Fritts, 1976) extending from the prior May to the current September of growth. The extension of the correlation analyses back into the prior growing season allowed for the possibility of climatic preconditioning on growth the following year. This is a very common phenomenon in tree-ring response functions (Fritts, 1976).

Figure 39.6 shows the correlation analysis results for each plantation. Most months do not show any correlation between climate and loblolly pine radial growth, especially during the prior growing season months. However, certain features are relevant to our purposes. For example, the two most western plantations (36 and 40), indicate a very high sensitivity to rainfall and maximum temperatures in June of the current growing season. The positive correlation with rainfall and negative correlation with maximum temperature during that month is a classic "drought sensitivity" response. That is, overall radial growth is less when June is dry and hot, particularly during the daylight hours when the trees are photosynthetically active. In the subsequent months of July to September, the sensitivity to both precipitation and temperature diminishes, although the signs of the correlations remain consistent with drought sensitivity and are sometimes statistically significant. Plantation 29, which is also a westerly, continental-interior site, also shows a drought response during current-June, but it is somewhat weaker compared to plantations 36 and 40. Precipitation during the earlier months of December, February, and April also appears to be influential on radial growth, but it is difficult to interpret this collective relationship causally other than to say that it may be related to soil-moisture recharge. Together, these results suggest that drought, particularly when it peaks in June, is an important growth-limiting factor to loblolly pine as it approaches its western range limit and probably contributes strongly to the lack of establishment and survival of this species beyond that limit. Although not terribly surprising, this conclusion is obviously relevant to concerns about possible increasing drought frequency in the southeastern United States resulting from greenhouse warming (Rind et al., 1990) and its consequent impact on forests. Loblolly pine would appear to be highly vulnerable in this regard.

The drought sensitivity of loblolly pine diminishes quickly for the plantations at more coastal and easterly locations. Plantations 28 and 32, which are still westerly but more coastal, show no sensitivity to June climatic conditions. At best, there is a weak dependence on spring climate and prior-November maximum temperatures at these plantations, but none are strong enough to warrant much attention. Plantations 07 and 15 indicate a later current growing season (mainly July) drought response, but this response is weaker than that found in plantations 36 and 40.

Plantation 03 has an unusual climate response that stands out from the others, that being significant correlations with January and February temperatures. This unusual result may be related to the comparatively cold January and February temperatures that this plantation experiences (see Figure 39.2). Given that this is the only plantation with mean maximum January and February temperatures

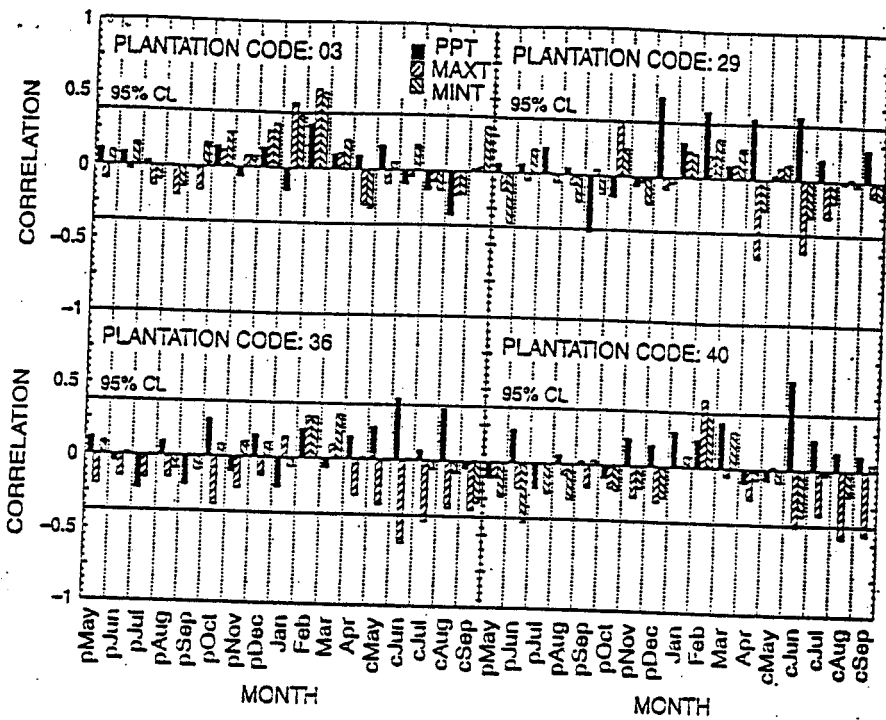


Figure 39.7. Correlations between loblolly pine trees of the local seed source and monthly climate for four extreme locations in the range of loblolly pine where adaptations of local seed sources to climate might be most evident. A comparison of Figure 39.7 with the relevant plantations in Figure 39.6 shows that there is no discernible local seed source adaptations.

below 10 °C, it is possible that this represents a threshold effect whereby loblolly pine is increasingly sensitive to winter injury, either through direct freezing or desiccation. Consequently, this finding may help explain how climate influences the northern range limit of this tree species.

We also examined the local seed source response to climate at each plantation to see if there was any evidence for local adaptations to the climatic environment. Figure 39.7 shows the results for four of the most extreme plantations: 03, 29, 36, and 40. By comparing Figure 39.7 with Figure 39.6, it is apparent that the local seed sources are not differentially adapted to climate in any obvious way, a result that is wholly consistent with similarity of the tree-ring chronologies themselves. Again, there seems to be little evidence for any meaningful differences between the seed sources.

Summary

This study has used the tree rings from a long-term common garden experiment to determine if there is any differential sensitivity of loblolly pine to climatic effects

at the seed source level. Based on the ANOVA results, there does appear to be a very weak differential sensitivity to climate at most of the SPSSS plantations. However, this effect is very small in terms of explained variance and is, for all practical purposes, meaningless. This essentially negative result was surprising given the clear differences in seed source performance over geographic space when viewed in terms of mortality, growth, and yield (Wakeley, 1953, 1959, 1961; Wells and Wakeley, 1966; Nance and Wells, 1981; Wells, 1969, 1983). However, it must be pointed out that the level of year-to-year variance in growth provided by the tree rings is typically a small fraction of that resulting from changes in absolute growth, especially during the juvenile and early maturation phases when growth rates are changing rapidly because of intense competitive pressures. Most of the SPSSS five-year remeasurements were made during that very active phase of plantation establishment and maturation.

The lack of any clear differential sensitivity to climate at the seed source level may be the result of the high level of noise or random variability between trees within seed sources, as pointed out earlier. It is difficult to know whether this noise is caused by truly random within- and between-plot effects or to the inherent genetic variability of the seed sources used. It is probably a combination of both effects. Regardless, the net effect was that the within-plantation seed source chronologies were practically identical after the within- and between-tree effects were averaged out over plots. As a consequence, the climate modeling could only be relied upon to provide a plantation-level expression of the response of loblolly pine to climate.

Perhaps the most practically useful results of this study have come from the plantation-level climatic response functions. There is a clear indication of increasing drought sensitivity of loblolly pine as it approaches the western limits of its range. This is indicated especially well for plantations 36 and 40 in east Texas and southwest Arkansas, respectively. Interestingly, the critical month in both cases is June when loblolly pines are especially sensitive to moisture availability and evapotranspiration demand. Any increase in drought frequency and severity resulting from greenhouse warming, especially during late spring and early summer, would have a devastating impact on these plantations and, by extension, loblolly pines growing elsewhere in this part of the range. For the more interior-range plantations (15, 28, and 32), overall climate sensitivity appears to be much weaker. However, given the lack of any meaningful seed source differences in climate response, it is clear that these plantations would also be vulnerable to any increase in drought frequency and severity as well. This conclusion is also supported by independent climatic response function analyses of loblolly pine tree-ring chronologies from Alabama (Jordan and Lockaby, 1990) and Georgia (Grissino-Mayer et al., 1989). In both cases, strong statistical evidence for growing-season drought sensitivity was found.

The climate response of plantation 03 in eastern Maryland is equally interesting for a different reason. In this case, the cardinal climate variables influencing radial growth are January and February maximum and minimum temperatures, with growing-season climate variables having little or no influence on growth. This

odd response may be related to a threshold effect in which maximum temperatures below 10 °C have a strong impact on radial growth potential. This result suggests that loblolly pine at the northern limit of its range may actually benefit from greenhouse warming during the winter, at least up to some level. However, from the analyses of the other plantations, it is clear that this benefit would occur only if the warming does not exceed ~ 4 to 5 °C during the winter months. Above that, the benefit would probably be lost and the Maryland trees would begin to respond more similarly to other plantations. It also suggests that loblolly pine will have the potential to move northward from its present northern range limit, either naturally or by artificial means, if future warming occurs. This movement would probably not go much beyond the ~ 5 to 6 °C January and February maximum temperature isotherm as it too moves northward, however.

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